

## Macrocephalic Male Bees as Functional Reproductives and Probable Guards

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*Abstract.*—In the Australian halictine bee *Lasioglossum (Chilalictus) erythrurum*, males are dimorphic; both typical males and large, disproportionately shaped, flightless males occur. The large, macrocephalic males fight with one another for exclusive occupancy of a communal nest and mate with females contained therein. They may also guard against predatory ants, and appear to be fed via oral trophallaxis by females.

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More or less isometric size variation among male bees occurs in thousands of species (e.g., Bego and de Camargo, 1984; Alcock et al., 1977). In males of some ground-dwelling, halictine and andrenid bees, however, size variation is accompanied by striking variation in shape (Sakagami et al., 1966; Knerer and Schwarz, 1978; Houston, 1970; Rozen, 1970; Hirashima, 1965). The extreme morphs are on one hand a typical male bee and, on the other, a morph with a disproportionately large head and mandibles, reduced wings, and a broad thorax (Sakagami et al., 1966; Houston, 1970). In some species, such as *Lasioglossum (Chilalictus) erythrurum*, variation in shape takes the form of two discrete morphs and only the extremes are found. In these cases the large, flightless, macrocephalic morph dwells in the nest.

Speculation concerning the function of these unusual males has suggested several hypotheses: (a) the presence of flightless, macrocephalic males is due to a behavioral “mistake” whereby a female places an unfertilized (male-producing) egg on a large, female-sized provision mass (Knerer and Schwarz, 1976, 1978), (b) these males represent a “soldier caste” (Houston, 1970), or (c) macrocephalic males are functional reproductives similar to those found in fig wasps (Hamilton, 1979). Here we present evidence concerning the role of the flightless, macrocephalic morph in nests of *L. erythrurum*.

### METHODS

We excavated 10 colonies of *L. erythrurum*. Each consisted of 10 or more adult females, female pupae, and zero ( $n = 1$ ), one ( $n = 8$ ), or two ( $n = 1$ ) macrocephalic males. No larvae or male pupae were present. One nest (containing a single macrocephalic) also contained the only normal male excavated. Presumably, many are present earlier in the season (a single, large nest excavated by M. S. in Nov. 1981 contained 15 adult females, 17 female pupae, 61 normal male pupae and 7 macrocephalic male pupae, 7 prepupae, and 63 larvae). Similarly, within the same species complex, Knerer and Schwarz (1978) report that for *L. (Chilalictus)*, sp. 1,

one nest contained 19 female pupae, 13 normal male pupae and 10 macrocephalic pupae and a second nest contained 44 female pupae, 23 normal male pupae and 17 macrocephalic male pupae). For this study, nests were taken from a loose aggregation on the Monash University campus near Melbourne, Australia during late February and March 1985, the time of year when mating and preparations for winter normally occur. The adults and pupae from these field colonies were used to establish artificial colonies in the laboratory, to provide a sample of females for dissection and as subjects in simple experiments.

Seven artificial nests (Michener and Brothers, 1971) were constructed to house colonies consisting of 10 females and a single macrocephalic male all from the same field nest. Two similar nests constructed of plaster-of-paris were used to obtain photographs upon which the line drawings in Figures 1, 2 and 3 are based.

After 10 days for equilibration, four nests were scan sampled every half hour from 9:00 a.m. to 4:00 p.m. for 5 days, and the first seen activity and location was recorded for each macrocephalic male. Continuous observation of 7 nests was carried out for a total of 27 hours over a three-week period.

Two experiments were conducted involving introduction of intruders into laboratory nests (see methods cited in Bell et al., 1974). First, macrocephalic males were introduced into nests already containing a resident macrocephalic male ( $n = 5$ ) and the interactions observed for 5 minutes. In one case, a male intruder was allowed by the experimenter to remain in the nest. Second, heterospecific intruders, female ants of the genus *Rhytidoponera*, were introduced into nests containing macrocephalic males ( $n = 3$ ) to determine if macrocephalic males would guard the nests against them. Interactions between macrocephalic males and ants were terminated after one minute to prevent injuries.

Virgin females (collected in the field as pupae and reared in the laboratory) were marked with LPC Office Products correction fluid and introduced into each of 3 nests that contained one macrocephalic male each (total = 6 females, two per nest). After 24 hours they were removed and dissected to determine the contents of the spermathecae. These dissections were conducted on freshly frozen females in Ringer's solution using a stereomicroscope. In addition, up to 10 females from each of 5 natural colonies were dissected ( $n = 37$ ) and the contents of the spermatheca recorded; similarly, the reproductive system of two adult macrocephalic males was examined (see also Houston, 1970).

## RESULTS

Scan samples of macrocephalic male behavior within nests revealed that they spent most of their time sitting at a location where females or intruders entering or leaving the nest could be encountered, that is 3–5 cm below the nest entrance at the junction of the main tunnel with the first main side branch, but only 6% of their time at the nest entrance (see Table 1), the typical station for a female guard in other halictine species (Bell et al., 1974). Continuous nest observation and simple experimentation revealed qualitative information concerning male-male interactions and male-female interactions.

Encounters between macrocephalic males always resulted in fighting (Fig. 1). One intruder was allowed to remain in the nest, it was forced by the occupant to the bottom of the nest, and died within two days. Both macrocephalic males taken from a single field nest were placed in the same laboratory nest where they fought

Table 1. The percentage of time spent at particular locations in the nest and the percentage of time spent performing specific activities for macrocephalic male *Lasioglossum (Chilalictus) erythrurum* in artificial nests.

Location in Nest	%	Behaviors	%
Feeding chamber	4	Sitting	79
Nest entrance	6	Walking	9
Main tunnel	32	Interacting with females	5
Intersection of main tunnel with upper branch	45	Tunneling	5
Side tunnel containing females	6	Grooming	2
Side tunnel not containing females	1		
Not seen	6		

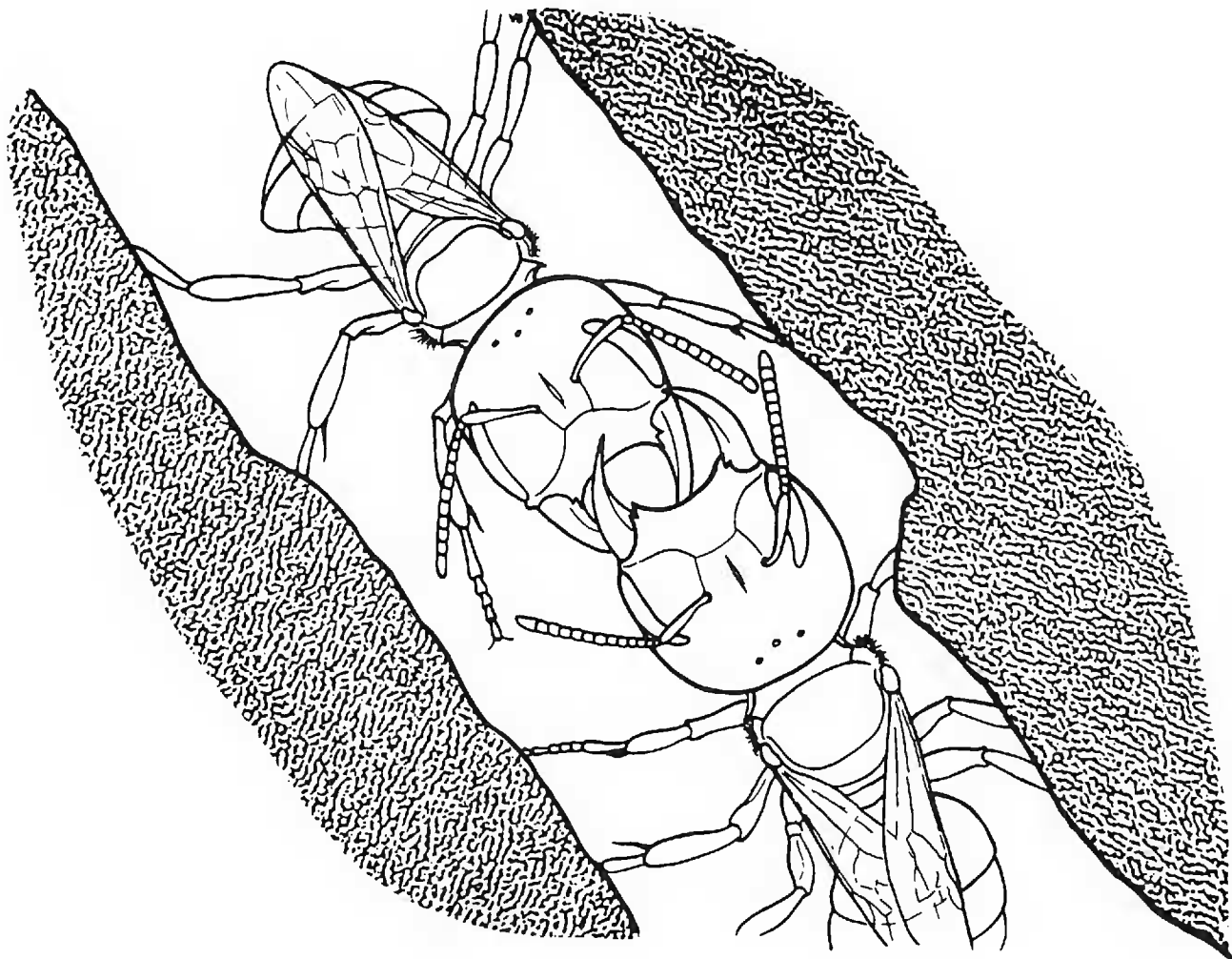


Figure 1. Macrocephalic *Lasioglossum (Chilalictus) erythrurum* males fighting within the nest.

repeatedly until one finally left the nest. These interactions explain why only one macrocephalic male was found in most field nests even though many are produced in each nest, and why dead macrocephalics were frequently found in nests during excavation. Macrocephalic males fight each other, apparently to the death, for the exclusive occupancy of a communal nest.

Observations of male-female interactions suggested that macrocephalic males are fed within the nest by females via oral trophallaxis ( $n = 3$ ; Fig. 2). More importantly, we observed mating taking place within the plaster nests ( $n = 2$ ; Fig. 3). Sperm was



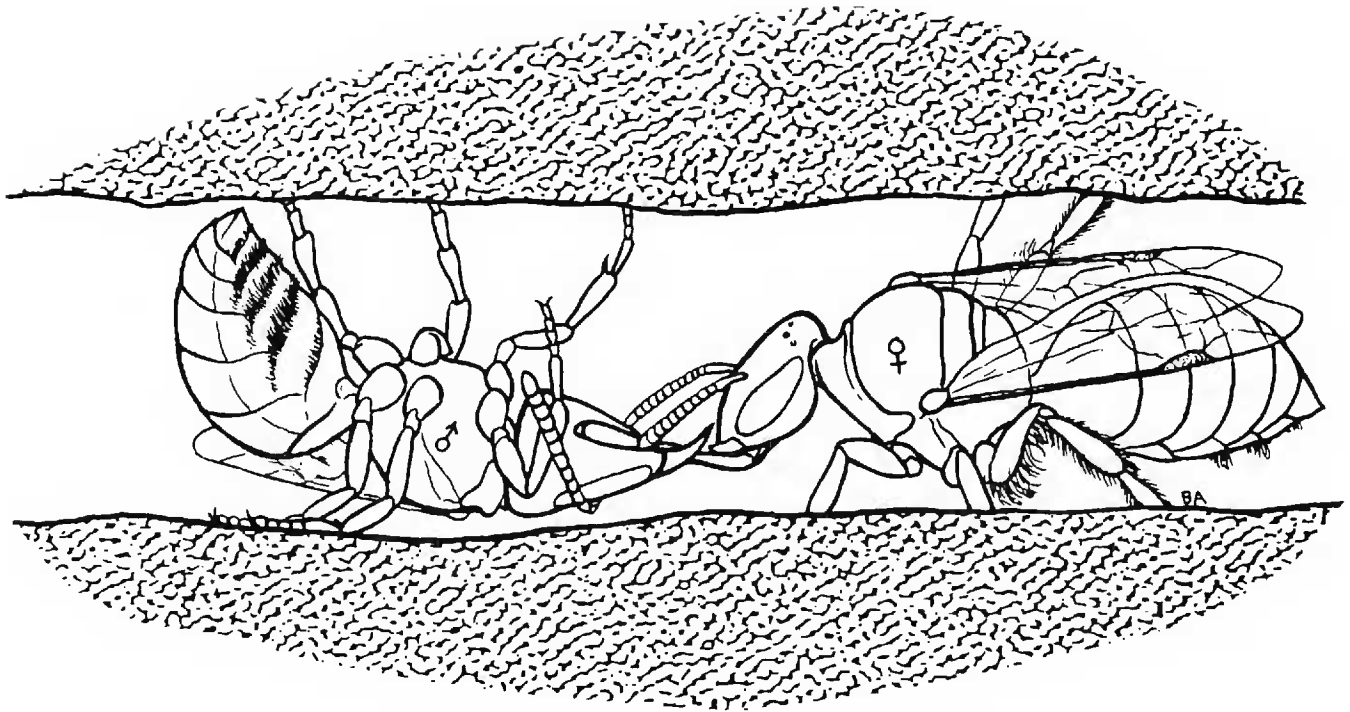


Figure 2. Apparent food exchange between male and female *Lasioglossum (Chilalictus) erythrurum* in the nest.

transferred during such matings. Of the 6 virgin females that were introduced into observation nests containing macrocephalic males, sperm was present in the spermathecae of all fully sclerotized (adult) females. Two teneral females with soft cuticles and very soft wings remained uninseminated. Most adult females collected from field nests occupied by a macrocephalic male contained sperm in their spermathecae (73%,  $n = 14$ ), while none from the field colony lacking a macrocephalic male were inseminated ( $n = 8$ ). Dissection of 2 macrocephalic males showed that they have normal-appearing reproductive systems containing motile sperm. This evidence shows that macrocephalic males of *L. erythrurum* are reproductively active within the nest.

There is also evidence that males may contribute to the welfare of the colonies with which they share a nest. They do a small amount of maintenance work within the nest. A small proportion of their time (5%) is spent in tunnel repair, both tamping earth into the side wall or moving it toward the entrance. More importantly, they may act as guards against heterospecific intruders. Macrocephalic males fought with intruding ants ( $n = 3$ ). On two occasions, macrocephalic males were seen to move toward intruding ants with open mandibles before contact was made.

#### DISCUSSION

In light of these results, the previously stated hypotheses can be evaluated. The first hypothesis set forth to explain this unusual situation is ontogenetic, asserting that the presence of flightless, macrocephalic males is due to a "mistake" whereby a female places an unfertilized (male-producing) egg on a large, female-sized provision mass, thus producing a morph for which no function exists. Since allometric growth patterns also occur in female halictine bees (Sakagami and Moure, 1965; Sakagami and Wain, 1966) and many highly social Hymenoptera (Wilson, 1953, 1985; Houston, 1976), the potential for developmental polymorphism appears

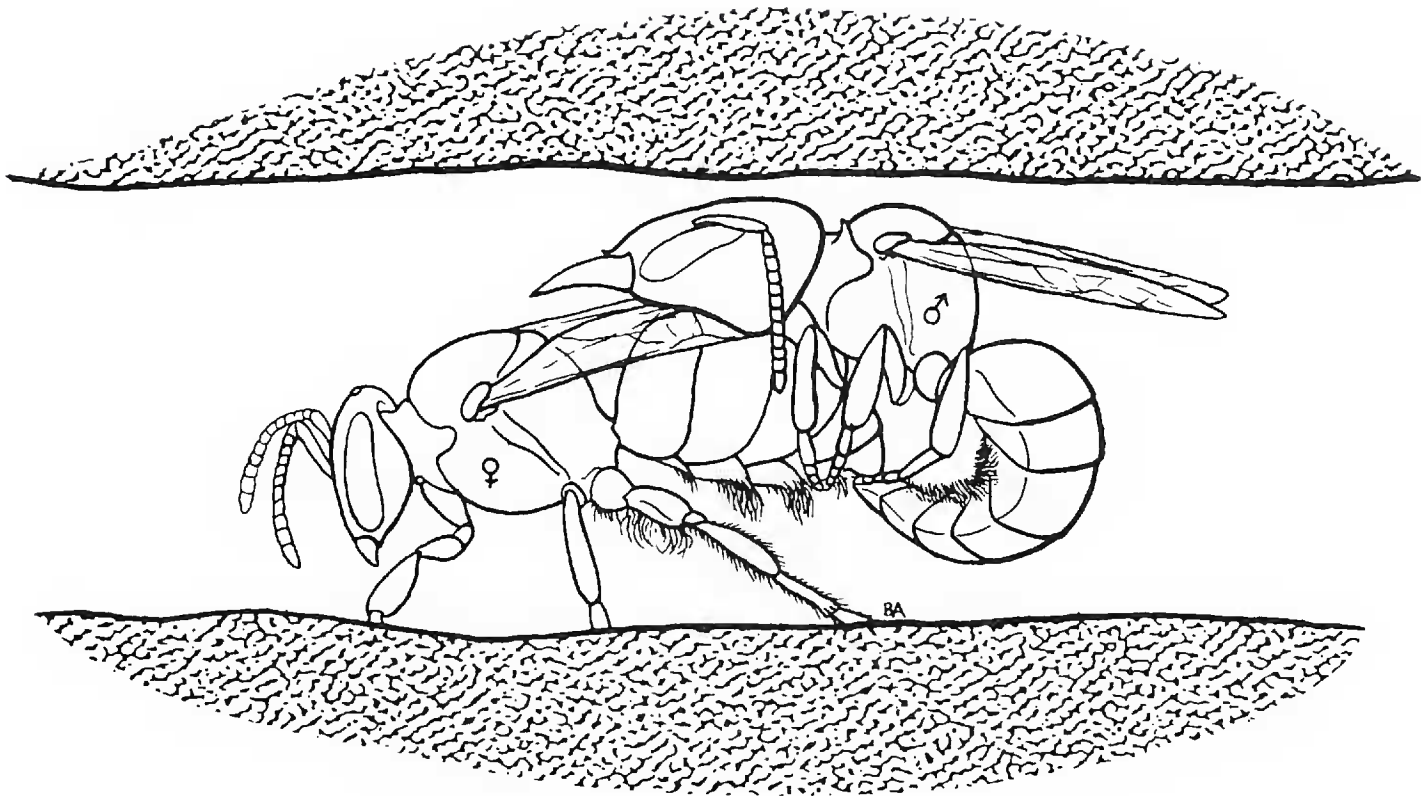


Figure 3. *Lasioglossum (Chilalictus) erythrurum* mating within the nest.

to be widespread. The mechanisms involved have received considerable attention, and studies support the hypothesis that allometric polymorphisms are due to environmental influences (e.g., nutrition) on development (Wilson, 1985).

Halictine bees are mass provisioners; within a brood cell a female prepares a provision mass from pollen and nectar upon which she deposits a single egg. Each cell contains only one individual, and the provision mass is completely consumed by the developing larva. The size of the provision mass and its composition determine larval nutrition and therefore control the size and perhaps morphology of the developing individual (Kamm, 1974).

Thus, this explanation is plausible at the mechanistic level. However, the presence of the extreme macrocephalic morph in certain species and its absence in closely related species (congeners) with similar sexual size dimorphism, plus the occurrence of intermediate forms in other halictine species (Sakagami et al., 1966) strongly suggest that the behavioral “mistake” hypothesis is not a full explanation.

The second, evolutionary-level, hypothesis suggests that the large morph persists because these males with large, powerful mandibles are an altruistic “soldier” caste, acting as “guards” for the communal nests they inhabit. This implies that such males are selected for via kin selection (Hamilton, 1964a, 1964b, 1972) through enhanced reproductive output of their relatives. Recent population genetics theory suggests that male altruism could evolve in the Hymenoptera under certain circumstances (Pamilo, 1984). However, in this case the evidence suggests that the contributions of flightless macrocephalic males to colony life through guarding behavior may be mate guarding, or a form of parental investment that provide individual fitness benefits with secondary benefits due to inclusive fitness. If a macrocephalic male has mated with females in the nest, he could be protecting his mates and through them his



offspring. Guarding by males occurs in solitary wasps in the genera *Oxybelus* (Peckham, 1977) and *Trypoxylon* (Brockman, 1980), and it reduces cleptoparasitism and appears to be associated with a direct reproductive role on the part of the guarding male. On the other hand, if females in the nest are relatives of the macrocephalic male, perhaps even mated to other males, he also could be increasing his inclusive fitness by protecting them.

Thus, it appears that the macrocephalic male morph gains in individual and inclusive fitness. It is of interest to note that extreme macrocephalic males are often found in the nests of other communal species such as *L. dimorphum* and *Perdita portalis* (Knerer and Schwarz, 1976, 1978; Houston, 1970; Rozen, 1970). A communal colony consists of a large number of females, not necessarily close relatives, each of which mates and produces brood. Perhaps mating is taking place within the nests of all these species and macrocephalic males are functional reproductives. With the possible exception of certain species of meliponine bees (Michener, 1974), and one halictine (Plateau-Quénu, 1959), it is commonly held that bees only mate outside their nests, a view that is supported by a large body of literature concerning the mating behavior of bees (Eickwort and Ginsberg, 1980; Alcock et al., 1978).

Flightless macrocephalic males in the communal nests of *L. erythrurum*, and perhaps other species of halictine and andrenid bees, are not "mistakes"; rather they are functional reproductives and perhaps also guards within their communal nests. Speculation concerning the evolution of this complex adaptation must wait until more information is available. Clearly, it involves selection acting on females who must allocate their reproductive effort. In *L. erythrurum*, females must produce an advantageous mixture of macrocephalic males, normal males and females. The role of normal males is not clear at present. Perhaps they obtain matings with females from nests that do not contain macrocephalic males or with females that remain unmated even from a nest occupied by a macrocephalic male. If there is a "penalty" for inbreeding, such as diploid male production, production of normal males might remain advantageous on the part of a female. In the halictine species *Lasioglossum zephyrum* diploid males are known to occur (Kukuk, unpublished data).

An additional question arises concerning the evolution of altruism in females. If many of the females in a single nest are inseminated by the same male, their offspring would be paternal half-sisters or full sisters and the relatedness among them would be at least 0.5. Since these females apparently then occupy and are reproductively active in the same nest, one might expect that a more hierarchical social system involving reproductive altruism would evolve under some cost/benefit situations; for example, if the costs of independent colony initiation are high. Detailed studies of the reproductive and social biology of communal species with intranidal mating are needed.

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